Functional Morphology and Evolution of the Genitalia of Diplopoda - Helminthomorpha

Andreas TADLER

Institut für Zoologie, Althanstr. 14, A-1090 Wien, Austria

ABSTRACT

Theories about the evolution of genitalia (lock and key, genitalia recognition, pleiotropy, sensory female choice, mechanical mate choice) make different predictions about the mutual coadaptation between male and female genitalia. In three species of Chordeumatida and four species of Julida different degrees of mutual mechanical coadaptation between male and female genitalia have been found. This supports EBERHARD's "Mechanical Mate Choice Theory". The "Pleiotropy Hypothesis" cannot explain the evolution of diplopod genitalia because pleiotropic effects are prevented by heterochrony.

RÉSUMÉ

Morphologie fonctionnelle et évolution des genitalia des Diplopodes Helminthomorphes.

Les théories relatives à l'évolution des genitalia ("clé-serrure", reconnaissance des genitalia, pléiotropie, choix sensoriel des femelles, choix mécanique de l'accouplement), font appel à différentes hypothèses prédictives sur la coadaptation des genitalia mâles et femelles. Chez trois espèces de chordeumatides et quatre espèces de julides, différents degrés de coadaptation mécanique entre genitalia mâle et femelle ont été définis. Ceci vient tout d'abord appuyer la théorie de EBERHARD du "choix mécanique de l'accouplement". L'hypothèse "pléiotrope" ne peut pas expliquer l'évolution des genitalia de diplopode car les effets pléiotropiques sont évités par l'hétérochronie.

INTRODUCTION

In many animal groups, the genitalia show an evolutionary pattern quite different from other morpho-anatomic structures. The most important questions concern the "rapid and divergent evolution" (EBERHARD, 1985) and the high degree of complexity of genitalia.

The male gonopods in the Helminthomorpha serve as a good example for the phenomena of diversity and complexity. There were no really fundamental changes in the peripheral phenotype of Helminthomorpha since the middle of the paleozoic (KRAUS, 1974), however, the gonopods have developed completely different functional principles and "*Bauplans*" in each order and family (VERHOEFF, 1928-32).

Theories, which have been formulated to answer the general questions about the evolution of genitalia lead to predictions about morphological complexity of female genitalia and mutual mechanical coadaptation between male and female structures (see EBERHARD, 1985 for discussion).

TADLER, A., 1996. — Functional morphology and evolution of genitalia in Diplopoda - Helminthomorpha. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 327-330. Paris ISBN : 2-85653-502-X.

The "lock and key" (DUFOUR, 1844, review: SHAPIRO & PORTER, 1989) and the "genitalic recognition" theories imply that sperm transfer between members of different species should be restricted. If a mechanical lock and key mechanism works, there should be a more or less tight mechanical fitting between male and female genitalia. In contrast, the genitalic recognition theory holds that heterospecific sperm transfer is avoided by species-specific stimulation. Therefore, the genitalia of females of different species should show differences in their sensory and nervous structures, but not in their morphology.

MAYR's "pleiotropy theory" (1963) proposes that genitalia are less subject to the corrective influences of natural selection and that changes in the structure of genitalia are caused by pleiotropic effects. The theory predicts that taxonomically important structural components of genitalia have no function. A tight mechanical correlation between male and female genitalia should not exist (KRAUS, 1968).

"Male competition" or "sperm competition" means that males can diminish the mating success of other males, for example, by displacing sperm from the receptacula of the female or by plugging the females' genitalia, so that the next male cannot deposit sperm (PARKER, 1970; SMITH, 1984). The theory predicts a rapid and divergent evolution of male genitalia, but no similar pattern in female genitalia.

The most recent theory is the "female choice theory " (EBERHARD, 1985). This theory supposes that females choose between males of their own species on the basis of genitalic structures. EBERHARD proposes two mechanisms, whereby female can discriminate between males:

1) Females discriminate between male genitalia on the basis of sensory structures, for example, mechanoreceptors. EBERHARD speaks about "internal courtship". Complexity of male genitalia arises because males evolve more and more efficient stimulatory organs. The theory predicts a rapid and divergent evolution of only male genitalia; female genitalia should be morphologically rather simple.

2) Females discriminate between male genitalia only by the mechanical fit. If genitalia mechanically fit well, then the probability of successful sperm transfer is high. This mechanical mate choice theory predicts that a morphological co-evolution between male and female organs occurs (EBERHARD, 1985).

GENITALIA FITTING IN DIPLOPODA

Analysis of diplopods frozen instantly during copulation shows that male gonopods do not represent simple casts of the female structures, but that there are different degrees of mutual mechanical coadaptation between male and female genitalia.

In *Nemasoma varicorne* (Julida, Nemasomatidae) the central area of the vulvae is modified to fit with the male solenomerit. In *Brachyiulus bagnalli* (Julida, Brachyiulidae), and *Cylindroiulus boleti* (Julidae, Cylindroiulinae) slits on the bursae of the female vulvae correspond to projections on the male gonopods. The female opercula of *Unciger foetidus* and *Cylindroiulus boleti* are modified to the different mechanical forces of the male pro-mesomerit forceps (HAACKER & FUCHS, 1970; TADLER, in press).

In three species of Chordeumatida different parts of the female vulvae are modified to fit with male parts.

On the vulvae of *Haploporatia eremita* (Mastigophorophyllidae), the margin bulge is enlarged. On the distal part of the anterior gonopods of the male, there are wing-like structures. In copula, the wing-like structures of the male gonopods fit between the margin bulge and the bursa of the female. In *Mastigona bosniense* (Mastigophorophyllidae), the basis of the vulvae is modified, so that during copulation the bursa can be rotated for more than 270 degrees. The sperm transferring distal part of the anterior gonopods is pressed by the basis against the openings of the receptacula (TADLER, 1989).

In *Craspedosoma transsilvanicum* (Craspedosomatidae) projections on the anterior gonopods of the male (terminal projection and clasping projection of the cheirite) insert into invaginations of the oviduct. During copulation the bursa of the female is pulled out from the vulval sac, the openings of the receptacula are thereby pressed against the sperm transferring parts of the male gonopods (brushes of the syncoxite) (TADLER, 1993).

DISCUSSION

The theories mentioned above are more or less mutually compatible. Genitalia could be influenced therefore by different evolutionary patterns.

According to the present observations, the most important factor for the evolution of genitalia of Helminthomorpha seems to be mechanical mate choice. Following MAYNARD SMITH (1987) female choice exists when some behaviour or structure of females causes them to mate more successfully with some males than with others. Therefore, even the simple evolutionary adaptation of male genitalia to female genitalia can be regarded as caused by female choice. It is important that the general theoretical models of female choice (FISHER, 1930; LANDE, 1981; BORGIA, 1987; POMIANKOWSKY, 1988) show that female choice concerns not only the evolution of male traits but also the evolution of female preferences. In our examples, change in female preference also means changes in female genital morphology. Therefore, the mechanical mate choice theory can explain the mutual mechanical adaptation of male and female genitalia (EBERHARD, 1985). Mechanical and sensory female choice may work together in Diplopoda, but unfortunately there is almost no information on the sensory structures of diplopod vulvae. Sensory female choice must therefore be examined by neuro-morphological and neuro-physiological studies.

The mechanical coadaptation between male and female genitalia may also be an indication that a lock and key mechanism works, but, of course the hypothesis must be tested, especially with regard to precopulatory isolation mechanisms.

A possible mechanism of sperm displacement has been found recently in a spirostreptid (BARNETT, TELFORD & DE VILLIERS, 1991), and there are even older observations, which suggest, that sperm competition exists in Diplopoda. For example the secretion caps (or "Kappenspermatophoren") described by VERHOEFF (1910) for the Chordeumatid *Mycogona germanica* may in fact be mating plugs. Sperm competition may be an important factor for the evolution of gonopods, however, it cannot explain the mechanical co-evolution between male and female genitalia.

PLEIOTROPY HYPOTHESIS

The existence of mutual mechanical coadaptation between male and female genitalia suggests that the pleiotropy hypothesis is less important.

For diplopods, one can turn the pleiotropy hypothesis around to arrive at a more plausible story. The two major groups of Diplopoda-Helminthomorpha, the Colobognatha and the Eugnatha, show great differences in the complexity and morphological diversity of gonopods. Whereas the gonopods of colobognaths are rather uniform and similar to walking legs, the gonopods of Eugnatha show a fantastic complexity and variety of forms (VERHOEFF, 1928-32). This may have to do with the ontogeny of the gonopods. Walking legs and gonopods are homologuous structures, but in Eugnatha, there is a heterochrony in the development of walking legs and gonopods. The legs of the seventh trunk unit of immature males either disappear entirely during post embryonic development or develop in to undifferentiated bumps (ENGHOFF, 1984).

It seems unlikely that in a metameric animal mutations would effect only a single segment. If there is no heterochrony, pleiotropic effects between gonopods and walking legs should be present. If, for example a mutation arises, which would have an advantageous effect for the gonopods, perhaps because it makes an additional projection on the tarsus, the same mutation would be very disadvantageous for walking legs. The rapid and divergent evolution of complex gonopods in Eugnatha is perhaps made possible, since heterochrony prevents pleiotropic effects between the peripheral phenotype and the gonopods.

ACKNOWLEDGEMENT

I thank Peter ZULKA for many discussions and for converting the paper to a Macintosh Computer.

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